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Production of Total Potentially Soluble Organic C, N, and P Across an Ecosystem Chronosequence: Root versus Leaf Litter

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Abstract

Dissolved organic matter (DOM) plays several important roles in forest ecosystem development, undergoing chemical, physical and/or biological reactions that affect ecosystem nutrient retention. Very few studies have focused on gross rates of DOM production, and we know of no study that has directly measured DOM production from root litter. Our objectives were to quantify major sources of total potentially water-soluble organic matter (DOM_{tps}) production, with an emphasis on production from root litter, to quantify and compare total potentially soluble organic C, N, and P (DOC_{tps}, DON_{tps}, and DOP_{tps}) production, and to quantify changes in their production during forest primary succession and ecosystem development at the Mt. Shasta Mudflows ecosystem chronosequence. To do so, we exhaustively extracted freshly senesced root and leaf and other aboveground litter for DOC_{tps}, DON_{tps}, and DOP_{tps} by vegetation category, and we calculated DOM_{tps} production (g m^{-2} y^{-1}) at the ecosystem level using data for annual production of fine root and aboveground litter. DOM production from throughfall was calculated by measuring throughfall volume and concentration over 2 years. Results showed that DOM_{tps} production from root litter was a very important source of DOM_{tps} in the Mount Shasta mudflow ecosystems, in some cases comparable to production from leaf litter for DON_{tps} and larger than production from leaf litter for DOP_{tps}. Total DOC_{tps} and DON_{tps} production from all sources increased early in succession from the 77- to the 255-year-old ecosystem. However, total DOP_{tps} production across the ecosystem chronosequence showed a unique pattern. Generally, the relative importance of root litter for total fine detrital DOC_{tps} and DON_{tps} production increased significantly during ecosystem development. Furthermore, DOC_{tps} and DON_{tps} production were predominantly driven by changes in biomass production during ecosystem development, whereas changes in litter solubility due to changes in species composition had a smaller effect. We suggest that DOM_{tps} production from root litter may be an important source of organic matter for the accumulation of SOM during forest ecosystem development.

Key words: belowground production; dissolved organic carbon (DOC); dissolved organic nitrogen (DON); dissolved organic phosphorus (DOP); fine root litter; temperate forest primary succession.

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Shauna M. Uselman, Robert G. Qualls, and Juliane Lilienfein conceived of or designed the study and performed research. SMU analyzed data and wrote the article. SMU and RGQ contributed new methods or models.

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Introduction

Dissolved organic matter (DOM) plays several important roles in forest ecosystem development, undergoing chemical, physical and/or biological reactions that affect ecosystem nutrient retention. DOM affects soil structure (by coating soil particles), transports Fe and Al in the process of podzolization (Pohlman and McColl 1988), transports organic contaminants (for example, herbicides, Cox and others 2007), and provides a potential C source for microbial growth (McDowell and others 2006). DOM may be particularly important to the development of a deepening distribution of soil organic matter (SOM) during ecosystem development (Sollins and others 1983; Lilienfein and others 2003). Forest ecosystems lose C, N, and P through the leaching of DOM which affects their overall budget (Qualls 2000). Most N and P losses from forest ecosystems are in the organic form (DON and DOP), particularly in areas that have not been impacted by acid rain or soil erosion (Sollins and McCorison 1981; Hedin and others 1995). As a result, the importance of DOM as a major N export from ecosystems is increasingly being recognized and studied (Perakis and Hedin 2002; Van Breemen 2002).

Although the importance of DOM in ecosystem function has become a topic of interest in recent years (for example, Kalbitz and others 2000; Qualls 2000; McDowell 2003), there are critical gaps in our understanding of controls on DOM in ecosystems. For example, in their 2000 review of controls on the dynamics of DOM in soils, Kalbitz and others listed quantification of DOM sources, including ''recent litter'' and ''root-derived DOM,'' as the first of seven future research needs. To date, we know of no study that has directly measured DOM production from root litter, although studies have examined DOM inputs from live root exudation (for example, Smith 1976; Uselman and others 2000). Furthermore, root trenching studies have suggested the importance of root-derived DOM (Aitkenhead-Peterson and others 2003; Lajtha and others 2005). In a paper on future directions for DOM research in soils, McDowell (2003) also highlighted the need to quantify DOM sources, including gross rates of DOM production in soils. Most measurements of DOM production from leaf litter represent *net* rates, measured as net fluxes of DOM from the bottom of the forest floor. DOM produced in the forest floor may be retained within the forest floor by adsorption, mineralization by microorganisms, or uptake by vegetation, prior to the emergence of net DOM at the boundary of the organic and mineral soil layers. In this study, we quantify gross production of DOM from litter by exhaustively extracting total potentially water-soluble organic matter (DOM_{tps}) and scaling to the ecosystem level using our measurements of above- and belowground litter production (Uselman and others 2007a). The reason we measure gross production of DOM is because it is important to understand the *supply* of DOM to the ecosystem, and it would be useful for modeling DOM inputs, (for example, Currie and Aber 1997). Our approach is analogous to other studies of primary productivity and detrital production, in that they are a measure of supply to the ecosystem. Furthermore, in separating the water-soluble from the insoluble component, we are taking a similar approach to studies that divide detrital production into various chemical components, for example lignin and cellulose. We use the terms ''DOM_{tps}, DOC_{tps}, DON_{tps}, or DOP_{tps}'' specifically to refer to total potentially water-soluble organic matter, C, N, or P that is soluble or could become soluble from solid organic matter originating from primary production. We do not address the fate of DOM in this study, but we examined the fate of DOM (leaching, adsorption, and respiration) originating from leaf versus root litter in a companion column study (Uselman and others 2007b).

Carbon originating from fine roots continues to be poorly understood, and yet this belowground input of nutrients may be of equal or greater magnitude than input from aboveground litterfall. In a companion study, we found that fine root production contributed from 14 to 49% of total fine detrital production (defined as root production + leaf litterfall) in a Ponderosa pine-mixed conifer forest ecosystem chronosequence at the Mt. Shasta Mudflows Research Natural Area in northern California (Uselman and others 2007a). Studies in other temperate pine forests have found production of fine roots to be of similar magnitude to aboveground litterfall production (Nadelhoffer and Raich 1992; Gower and others 1996), and Vogt and others (1996) have suggested that root production may contribute up to 50% of the C annually cycled in forests. As a consequence, root litter could potentially contribute large amounts of soluble organic nutrients to forest ecosystem cycling in the form of dissolved organic carbon (DOC), dissolved organic nitrogen (DON), and dissolved organic phosphorus (DOP). In our study, we include DON and DOP because much less is known about the dynamics of DON and very little is known about DOP (Kalbitz and others 2000; McDowell 2003).

We examine DOM_{tps} production from all major sources (that is, from fine root litter, aboveground

litterfall, and throughfall) along an ecosystem chronosequence at the Mt. Shasta Mudflows Research Natural Area, building on classic studies of primary succession and soil development by Dickson and Crocker (1953a, b, 1954). Increases in SOM have been observed in primary succession studies in general (Schlesinger 1991), and previous work at the Mt. Shasta site has shown that DOM may play a role in the accumulation and deepening distribution of SOM (Sollins and others 1983; Lilienfein and others 2003, 2004a). Although changes in DOM production during primary succession and ecosystem development should, in theory, be affected primarily by changes in net primary production (NPP), differences in litter chemistry of different species may also affect DOM production (Pohlman and McColl 1988). At the Mt. Shasta site, we found that aboveground litterfall and fine root production generally followed a pattern where maximum production was reached early in the chronosequence of ecosystem ages (Uselman and others 2007a). Though we expect to find DOM_{tps} production will follow similar patterns as litter *biomass* production during primary succession and ecosystem development, we also expect to find that DOM_{tps} production may be affected by changes in species composition during succession.

Our study had two primary objectives

(1) To quantify and compare major sources of DOM_{tps} production (as DOC_{tps}, DON_{tps}, and DOP_{tps}) from three main sources (freshly senesced fine root litter, freshly senesced aboveground litter, and throughfall). We hypothesized that DOM_{tps} production from freshly senesced fine root litter is greater than DOM_{tps} production from freshly senesced leaf litter (in units of g m^{-2} y^{-1}).
(2) To quantify changes in DOM_{tps} production during primary succession and ecosystem development. We hypothesized: (a) that DOM_{tps} production increases early in primary succession, because of increases in litter *biomass* production, (b) that the relative contribution of belowground DOM_{tps} production to total fine detrital DOM_{tps} production increases along the ecosystem chronosequence, and (c) that DOM_{tps} production is affected by shifts in species composition, as illustrated by DOM_{tps} production from freshly senesced leaf litter.

We tested these hypotheses by measuring annual fine root and aboveground litter production over one or 2 years, respectively (Uselman and others 2007a), by exhaustively extracting freshly senesced root and aboveground litter for total potentially water-soluble organic C, N, and P by vegetation category, and by measuring throughfall volume and concentration over 2 years, across an ecosystem chronosequence.

Methods

Definitions

We use the terms DOM_{tps}, DOC_{tps}, DON_{tps}, or DOP_{tps} to refer to total potentially water-soluble organic matter, C, N, or P that is soluble or could become soluble from solid organic matter. Additionally, we use the terminology of ''DOM_{tps} *content*'' of litter to refer to ''total potentially soluble organic matter'' in units of mg g^{-1} dry weight.

Study Area and Experimental Design

The study area is located on an ecosystem chronosequence within the Mt. Shasta Mudflows Research Natural Area, about 6 km NE of McCloud, California, USA. Mudflow ages were 77, 255, 616, and >850 years old in 2001 (see Dickson and Crocker 1953a; Lilienfein and others 2003; and Uselman and others 2007a). Topography, aspect, climate, and parent material are uniform across the chronosequence (Lilienfein and others 2003). Young soils are Typic Haploxerepts and older soils are Humic Vitrixerands (Qualls and Bridgham 2005). Flows are first dominated by Ponderosa pine forest, which later develops into mixed-conifer forest during primary succession and ecosystem development (as detailed in Dickson and Crocker 1953a). Climate can be generalized as winter precipitation—summer drought temperate, with an average precipitation of 1300 mm, falling mainly as snow (November to March) (Lilienfein and others 2003). Additional site details can be found in Dickson and Crocker (1953a), Sollins and others (1983), Lilienfein and others (2003), and Uselman and others (2007a).

Five to six plots (10 × 10 m) were located across each of the mudflows (20–21 plots total), according to a stratified random sampling design, randomly offset from transects. In three of the mudflows, we allocated 5 plots along 700–800 m transects, but because the 255-year-old mudflow exists as remnant ''islands'' (see Sollins and others 1983), we allocated 6 plots to this mudflow (3 plots randomly chosen within each of two approximately 3 ha areas). All plots were located within a 50 m elevation range and were within 3 km of each other. Areas of obvious disturbance, non-representative forest, or shallow mudflow depth were rejected.

No charcoal was observed in the forest floor within the plots. Initially, the six plots in the 255-year-old ecosystem were chosen pending further soil analyses. When chemical analyses verified that all plots exhibited characteristics of the 255-year-old mudflow, all plots were included in the larger study. Five plots (×4 flows = 20 plots total) were used for the root study, but all plots (21 plots) were used for aboveground litter and throughfall. More detailed information about plot selection can be found in Lilienfein and others (2003) and Uselman and others (2007a).

Total aboveground litterfall (sorted into leaves of each species, woody litterfall, and reproductive parts), measured 2 years (2000–2002), and total fine root production, measured 1 year (2001–2002), were reported in Uselman and others (2007a). These data were used to scale above- and belowground DOM_{tps} production to the ecosystem level for this study.

Sample Collection of Freshly Senesced Fine Root and Leaf Litter

We collected freshly senesced fine roots from root ingrowth cores that we used to measure total fine root production (Uselman and others 2007a). These roots are *freshly senesced fine roots*, as opposed to simply *dead fine roots*. We attempted to collect roots that had died recently to minimize DOM losses. DOM losses can be significant in initial leaf litter (Nykvist 1963) and we assumed that a similar phenomenon might occur with roots. These roots also have an upper age limit of 5–7 months, because we only used freshly senesced fine roots from the first harvest of root ingrowth cores (placed April and removed November, see Uselman and others 2007a).

As a comparison to freshly senesced fine roots, we also collected live fine roots from root ingrowth cores harvested over the course of 1 year (Uselman and others 2007a). It should be noted that these roots were live when sorted from the ingrowth cores, and they were severed from the tree at the time of harvesting. The reason for also using live fine roots for estimating DOM_{tps} production was to set an upper limit to our estimate of DOM_{tps} production from recently senesced fine roots. It is likely that DOM_{tps} production from fine root litter falls between these two estimates.

To minimize DOM losses from aboveground litter, we collected freshly senesced leaf (and other aboveground) litter that had never been rained on. This litter was collected on screens during peak litterfall (September–November continuously).

Exhaustive Sequential Extraction Procedure for Roots and Aboveground Litter

Collected roots were quickly washed in deionized water (and quickly sonicated if heavily mycorrhizal) to remove most soil. All collected aboveground litter and root samples were air-dried, coarsely ground (using a coffee grinder), and homogenized. Subsamples were finely ground in a ball-mill, to increase the rate of extraction of the potentially soluble organic matter (O.M.). By increasing the *rate* of extraction by grinding, we should not have affected our goal of completely extracting the *total* amount of water-soluble O.M. The soluble O.M. was exhaustively extracted by performing 8 sequential extractions, with a 1:100 ratio of dry mass to solution. This resulted in over 50% of the soluble content of the litter being extracted within one hour in the first extraction, suggesting that dissolution in the initial extraction is mostly limited by concentration gradient rather than time. A $HgCl_2$ solution (5 mg/l) was used for the extractions to suppress potential microbial activity during the extraction procedure because the extracts have been shown to contain an easily degraded component (Qualls and Bridgham 2005). A more highly concentrated $HgCl_2$ solution (20 mg/l) was found to inhibit dissolution of soluble O.M. The $HgCl_2$ solution had a pH of 6. One benefit of multiple extractions was that the pH of the first extraction with litter was 4.5, but it approached neutrality after several extractions, thus low pH would not limit the solubility of some compounds. The initial ground aboveground litter and root material was corrected for moisture content by oven-drying subsamples at 70°C to constant weight, and the root material was corrected for ash content by combusting subsamples at 450°C for 4 h.

For the first and second extractions, we added 0.3 g dry mass to 30 ml of $HgCl_2$ solution (5 mg/l) in 50 ml centrifuge tubes (or 0.1 g to 10 ml solution in 15 ml centrifuge tubes when less dry mass was available), placed the tubes horizontally on a gyro-rotary shaker for an hour, centrifuged at 22°C at 3650 rpm for 30 min, and filtered the supernatant through 0.45 μm membrane filters (GN-6, Pall Corp., Ann Arbor, MI). The supernatant was immediately frozen until analysis (into separate tubes for individual analyses). After each extraction, we carefully removed any particulate O.M. from the filter used on the previous extract and added it back to the pellet in the centrifuge tube. For each of the six following sequential extractions, we added 30 ml of fresh $HgCl_2$ solution to each

centrifuge tube (or 10 ml for smaller tubes), placed them on the shaker overnight, centrifuged, and filtered.

Calculations for DOM_{tps}

DOM_{tps} was calculated for each sample by fitting an exponential curve to the 8 data points (as cumulative DOM in mg g^{-1} dry weight) and calculating the asymptote. The following model for describing the accumulation of the product of a first-order reaction, as used for potential N mineralization by Molina and others (1980), was used to fit the data: $y = a\left(1 - e^{-kt}\right) + c$, where y is cumulative DOM_{tps} in mg g^{-1} dry weight, a is the asymptotic value of y, c is the y-intercept, and k is the rate of increase in y over extraction t. Essentially, the first extraction is the non-zero intercept, so DOM_{tps} is calculated by adding a + c.

For DOC, we fit a curve for each individual sample (8 extracts × 142 samples), calculated an asymptote, and corrected the sample to reflect DOC_{tps}. With 8 extractions, curve fits were excellent, with average R^2 values of 0.9975 ± 0.0002 and C.V. values of 1.8 ± 0.08% (overall means of all samples ± SE). The Appendix illustrates an example of two samples with a cumulative curve fit to the data points. In general, curve corrections (that is, the difference between the cumulative measured DOM content of the 8 extractions and the calculated asymptote) were less than 5% of the DOM_{tps} (4.2% for DOC_{tps}, 3.0% for DON_{tps}, and 3.7% for DOP_{tps}).

For DON and DOP, we analyzed all 8 extracts of a single sample of each litter category (composited from plots across the flows) and fit a curve to each litter category. Generally, curve fits for DON and DOP were excellent, with average R^2 values of 0.9970 ± 0.0008 for DON_{tps} and 0.9739 ± 0.0136 for DOP_{tps}, and C.V. values of 2.17 ± 0.21% for DON_{tps} and 10.22 ± 4.74% for DOP_{tps} (overall means of all category curves ± SE). From these curves, we found that the asymptote was approximately 3.0% for DON_{tps} and 3.7% for DOP_{tps} higher than the cumulative measured values in the first 8 extracts. Because these curve corrections were small and predictable, we could simply reduce the analyses for DON and DOP by compositing the 8 extracts for each individual plot, analyzing the composites, and applying the curve corrections (specific to each litter category) to estimate the asymptote.

It is important to note that if we had only extracted samples once, we would have only extracted 66 ± 1% of the DOC_{tps}, 64 ± 3% of the DON_{tps}, and 68 ± 4% of the DOP_{tps} (overall means ± SE), which would have resulted in very inaccurate estimates. This illustrates that DOM_{tps} content may be seriously underestimated by (1) using an insufficient number of extractions and/or (2) assuming that increased time of extraction could substitute for additional extractions.

Throughfall Collection and Flux Calculations

Throughfall was collected using polypropylene funnels with a cross-sectional area of 322.1 cm^2 connected to 4 L polypropylene bottles, placed approximately 120 cm above the ground. Over a period of 2 years (2000–2002), we collected throughfall monthly from two collectors in each plot, and we composited the two subsamples. Samples were filtered through 0.45 μm membrane filters (Pall Corp.) and frozen until analysis. Throughfall fluxes (in g m^{-2} y^{-1}) were calculated from volumes and concentrations. During winter months, throughfall was collected as snow that had fallen through the canopy, which was collected by coring and melted for analysis. To avoid overestimating DOM inputs from throughfall, we discarded cores that included visible litter. Volumes that melted during each interval were estimated from precipitation during the interval minus the change in snowpack liquid volume determined using snow cores. Precipitation in an open non-forested area was collected, filtered, and analyzed in a similar manner as throughfall samples. Open-area fluxes (in g m^{-2} y^{-1}) were calculated from measured concentrations multiplied by precipitation measurements at the McCloud weather station (6 km SW of the study site). Canopy leaching is defined as throughfall minus inputs from open-area precipitation.

Chemical Analyses of Extracts/ Throughfall and Solid Organic Matter

Extract and throughfall (and rainfall) solutions were analyzed for DOC concentration using a Shimadzu TOC-5050A Total Organic Carbon Analyzer (Shimadzu Corp., Columbia, MD). Concentrations of nitrate (NO_3^-) and ammonium (NH_4^+) were determined colorimetrically (Lachat 1997) using a Lachat QuikChem 8000 Flow Injection Auto-analyzer (Lachat Instruments, Milwaukee, WI). Total dissolved N (TDN) was analyzed after persulfate oxidation (Koroleff 1983) and NO_3^- analysis. DON was calculated by difference: DON = TDN − (NO_3^--N + NH_4^+-N). Orthophosphate (PO_4^{3-}) concentration was determined colorimetrically

with the molybdate blue/ascorbic acid method (Wetzel and Likens 1991) using a Shimadzu UV-1201 Spectrophotometer (Shimadzu Corp.), and total dissolved P (TDP) was analyzed after digestion with persulfate and PO_4^{3-} analysis (Wetzel and Likens 1991). DOP was calculated by difference: DOP = TDP − PO_4^{3-}-P.

Aboveground litter and root samples were analyzed for total C and N by dry combustion using a LECO TruSpec Analyzer (LECO Corp., St. Joseph, MI) and analyzed for total P by inductively coupled plasma emission spectroscopy (ICP) using a Spectro CirOs ICP Spectrometer (SPECTRO Analytical Instruments, Kleve, Germany) after dry ashing and dissolution in HCl at the Oklahoma State University Soil, Water, and Forage Analytical Laboratory (Stillwater, OK).

Production Calculations for DOM_{tps} from Litter

DOM_{tps} production (g m^{-2} y^{-1}) was calculated by multiplying DOM_{tps} content (mg g^{-1} dry weight) by total production of litter (g m^{-2} y^{-1}) by plot. Production was calculated separately for DOC_{tps}, DON_{tps}, and DOP_{tps}; separately for each litter category (root litter, live roots, leaf litter by species, woody litter, and reproductive litter); and separately for each ecosystem age. Aboveground DOM_{tps} production was calculated either as (1) DOM_{tps} production from total aboveground litterfall, or (2) DOM_{tps} production from leaf litterfall only. Belowground DOM_{tps} production was calculated either as (1) DOM_{tps} production from fine root litter (based on extractions of recently senesced fine roots), or (2) DOM_{tps} production from live fine roots (based on extractions of live fine roots). Total DOM_{tps} production was summed from canopy leaching, total aboveground litterfall, and fine root production. One total was calculated based on extractions of recently senesced fine roots and another based on live fine roots.

Statistical Analysis

Total Production of DOC_{tps}, DON_{tps}, and DOP_{tps}

Separate one-way ANOVAs and Tukey's HSD tests were used to test for differences among ecosystem ages for total DOC_{tps}, DON_{tps}, and DOP_{tps} production (separately for estimates using recently senesced or live fine roots).

Production of DOC_{tps}, DON_{tps}, and DOP_{tps} by Source

We also examined patterns in production of DOC_{tps}, DON_{tps}, and DOP_{tps} from each source during ecosystem development. To do so, we used individual one-way ANOVAs and Tukey's HSD tests, separately for each element (that is, DOC_{tps}, DON_{tps}, or DOP_{tps}) and for each source (that is, canopy leaching, aboveground litterfall, and fine roots) to test for differences among ecosystem ages. Production from leaf litterfall only was included for purposes of comparison to production from fine roots, which was calculated in one of two ways, either using live or recently senesced root extractions. To meet the assumptions of normality and equal variances, DOC_{tps}, DON_{tps}, and DOP_{tps} data were square-root transformed. Specifically, DOC_{tps} data were transformed by ($\sqrt{(X + 0.5)}$), and DON_{tps} and DOP_{tps} were transformed by ($\sqrt{(X)} + \sqrt{(X + 1)}$), which is best when X is 2 or less (Zar 1996).

Litter Mass

Litter mass data for each category were log transformed ($\log_{10}(X + 1)$) to meet assumptions of normality (Shapiro–Wilk test) and equal variances (Levene's test). Categories were tested for significant differences among ecosystem ages using separate one-way ANOVAs. When transformation still did not achieve equal variances, the Welch F-ratio was used, which corrects for unequal variances.

DOM_{tps} Contents of Litter and Percent Extractable DOM_{tps} of Litter

For each litter category, DOC_{tps}, DON_{tps}, and DOP_{tps} contents of litter (mg g^{-1} dry weight of litter) were tested for significant differences among ecosystem ages using separate one-way ANOVAs. Similarly, for each litter category, the percent extractable DOC_{tps}, DON_{tps}, and DOP_{tps} of litter (as percentages of total C, N, and P, respectively) were tested for significant differences among ecosystem ages using separate one-way ANOVAs. Individual ANOVAs containing data that violated the equal variances assumption were evaluated using the Welch F-ratio.

Leaf versus Root Litter Comparison

To test for differences in DOM_{tps} production from leaf litter and DOM_{tps} production from fine roots, we used separate 2-way split-plot ANOVAs for DOC_{tps}, DON_{tps}, and DOP_{tps}, where ecosystem age was the between plot factor and production source (that is, leaf or root) was the within plot factor. For each element, separate 2-way ANOVAs were performed: one comparing leaf to recently senesced root DOM_{tps} production, and one comparing leaf to

live root DOM_{tps} production. (Data were transformed as specified above for production by source variables.)

Differences between leaf versus root litter were also tested for the following six dependent variables: DOC_{tps}, DON_{tps}, and DOP_{tps} content of litter, and percent extractable DOC_{tps}, DON_{tps}, and DOP_{tps} of litter. For each variable, we calculated species-weighted average values for leaf litter (by plot). As explained above for DOM_{tps} production, we used separate 2-way split-plot ANOVAs for each of the six dependent variables to make the following comparisons: (1) leaf versus recently senesced root, (2) leaf versus live root, and (3) recently senesced root versus live root.

Ratio of DOM_{tps} Production from Root Litter to DOM_{tps} Production from All Fine Litter

Separate one-way ANOVAs and Tukey's HSD tests were used to test for differences among ecosystem ages for the ratio of DOM_{tps} production from root litter to DOM_{tps} production from all fine litter (separately for DOC_{tps}, DON_{tps}, and DOP_{tps}; and separately for estimates using recently senesced or live roots). Proportion data were transformed by arcsine ($\sqrt{p}$). Data were analyzed using SPSS, Inc. (2003, version 12.0 for Windows, Chicago, IL, USA) software.

Results

Patterns in DOM_{tps} Production Across Ecosystem Chronosequence

Total production (in g m^{-2} y^{-1}) of DOC_{tps} from all sources (that is, the sum of DOC_{tps} production from canopy leaching, total aboveground litterfall, and live or recently senesced fine roots) tended to be highest in the 255-year-old ecosystem (Figure 1). Total production of DON_{tps} based on live roots tended to be highest in the 255-year-old ecosystem, but there were no time trends for total production of DON_{tps} based on recently senesced roots. Total production of DOP_{tps} did not differ among ecosystem ages.

DOM_{tps} production from individual sources exhibited different patterns during ecosystem development (Figures 2–4). Production of DOC_{tps} and DON_{tps} generally followed similar patterns during ecosystem development. Although DOP_{tps} production patterns were similar to DOC_{tps} and DON_{tps} for fine roots, the pattern for aboveground litterfall was unique. DOM_{tps} production from total aboveground litterfall tended to be highest in the 255-year-old ecosystem for DOC_{tps}, showed no significant differences for DON_{tps}, and was significantly highest in the youngest 77-year-old ecosystem for DOP_{tps}. DOM_{tps} production from leaf litterfall was significantly highest in the 255-year-old ecosystem for DOC_{tps}, and showed no time trends for DON_{tps} and DOP_{tps}. Generally, DOC_{tps}, DON_{tps}, and DOP_{tps} production from recently senesced and live fine roots appeared to reach a maximum by the 255-year-old ecosystem, with the exception of DOC_{tps} production from live fine roots which continued to increase across the chronosequence.

Dissolved organic matter production from canopy leaching did not show any significant differences across the chronosequence, except for DOC where it was highest in the 616-year-old ecosystem. Open-area precipitation fluxes in g m^{-2} y^{-1} averaged 1.72 for DOC, 0.03 for DON, and 0.005 for DOP. Therefore, average canopy leaching fluxes were responsible for 79% of DOC, 80% of DON, and 73% of DOP throughfall fluxes across the ecosystem chronosequence.

Changes in Litterfall Composition Across Ecosystem Chronosequence

Leaf litterfall is separated by species and shows significant changes in species abundance over the ecosystem chronosequence (Table 1). These changes demonstrate the dominance of *P. ponderosa* in the youngest ecosystem and the shift to mixed-conifer forest in the older ecosystems.

Patterns in DOM_{tps} Content and Percent Extractable DOM_{tps} of All Litter Categories Across Ecosystem Chronosequence

In most cases, DOM_{tps} contents (in units of mg g^{-1} dry weight) of the leaf litter categories did not change significantly during ecosystem development, with the exception of DON_{tps} content of *Q. kelloggii* litter which increased from the 616-year-old to the >850-year-old ecosystems (Table 2). Although there were significant differences among ecosystem ages for some of the DOM_{tps} contents of fine roots, there were no consistent patterns with age. Reproductive litter showed a unique pattern in which the 77-year-old ecosystem was significantly different from the others: DOC_{tps} and DON_{tps} contents were lower, but DOP_{tps} content was higher. In general, reproductive litter DOP_{tps} contents were very high compared to other litter categories, especially in the 77-year-old ecosystem dominated by *P. ponderosa*.

Substantial proportions of the C, N, and P in a variety of types of litter were water-soluble

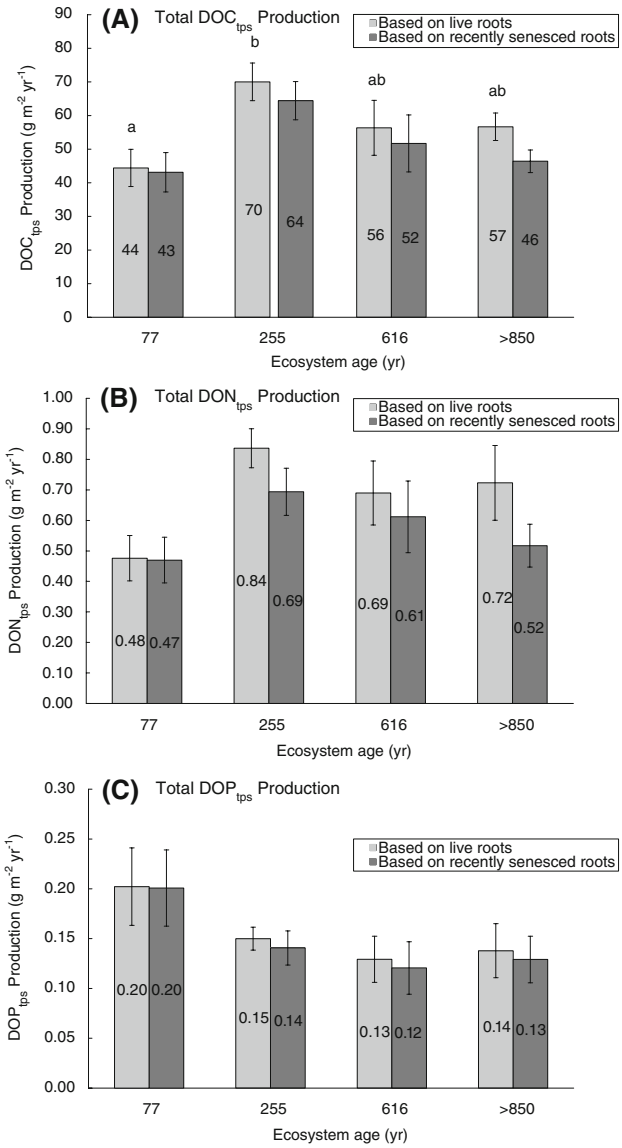

Figure 1. Total production of (**A**) DOC_{tps}, (**B**) DON_{tps}, and (**C**) DOP_{tps} (means ± SE in g m^{-2} y^{-1}) across an ecosystem chronosequence. Total production is the sum of DOC_{tps}, DON_{tps}, and DOP_{tps} production in canopy leaching, total aboveground litterfall, and fine root production, calculated separately either with fine root production based on live or recently senesced root extractions. Each bar represents the average of five replicate plots. The effect of ecosystem age is as follows: DOC_{tps} ($P = 0.06$, live; $P = 0.11$, recently senesced), DON_{tps} ($P = 0.09$, live; $P = 0.30$, recently senesced), and DOP_{tps} ($P = 0.26$, live; $P = 0.20$, recently senesced), based on separate one-way ANOVAs. Means with different letters are significantly different (separate Tukey's HSD tests, $P < 0.05$).

(Table 3). For example, 6–15% of the N in fine roots and 14–25% of the N in leaf litter was water-soluble. In general, trends in percent extractable DOC_{tps}, DON_{tps}, and DOP_{tps} of litter across the ecosystem chronosequence were similar to those for DOM_{tps} contents of litter, with a few exceptions (Table 3). For leaf litter, percent extractable DOP_{tps} of *A. concolor* increased significantly across the chronosequence. In two cases, there were significant differences among ecosystem ages for percent extractable DOM_{tps} of fine roots, but the patterns were not the same. For the reproductive litter category, there were no significant differences for percent extractable DOP_{tps}.

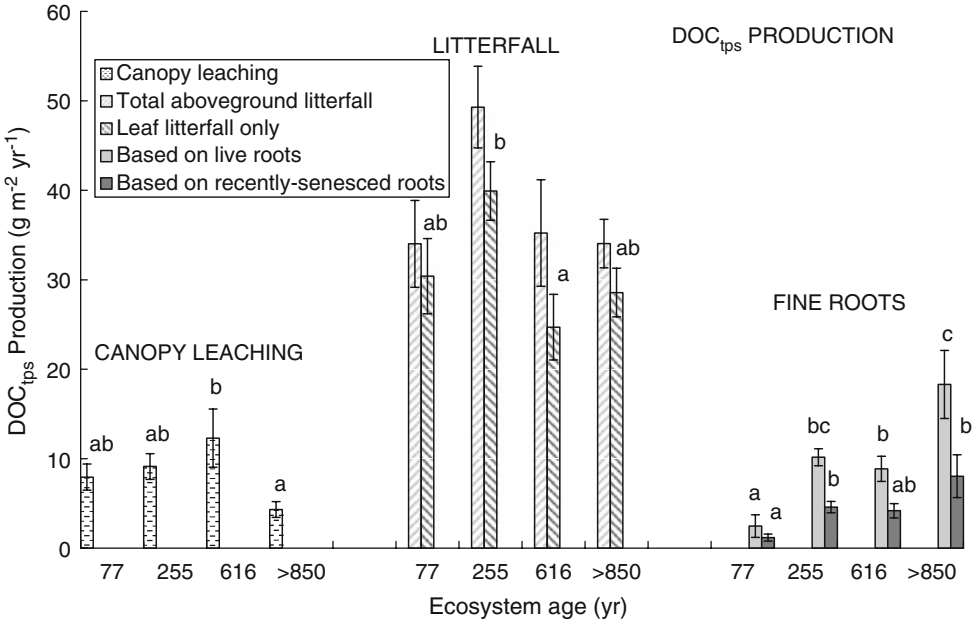

Figure 2. DOC_{tps} production from canopy leaching, total aboveground litterfall, leaf litterfall only, live fine roots, and recently senesced fine roots (means ± SE in g m^{-2} y^{-1}) across an ecosystem chronosequence. Canopy leaching is throughfall minus open-area precipitation inputs. Each bar represents the average of five (or six) replicate plots. Effect of ecosystem age is as follows: canopy leaching ($P = 0.05$), total aboveground litterfall ($P = 0.09$), leaf litterfall only ($P = 0.03$), live fine roots ($P < 0.001$), and recently senesced fine roots ($P = 0.002$), based on separate one-way ANOVAs (on square-root transformed data). Means with different letters are significantly different (separate Tukey's HSD tests, $P < 0.05$) compared within each source. Two-way ANOVAs indicate that DOC_{tps} production from leaf litter is significantly greater than production from recently senesced fine roots ($P < 0.001$) and live fine roots ($P < 0.001$).

Root versus Leaf Litter: Comparisons of DOM_{tps} Production, DOM_{tps} Content, and Percent Extractable DOM_{tps}

DOC_{tps} production (g m^{-2} y^{-1}) from leaf litter was 7.7 times greater than production from recently senesced fine roots, and DON_{tps} production from leaf litter was 1.5 times greater than production from recently senesced fine roots. In contrast, production of DOP_{tps} from recently senesced fine roots was 1.2 times greater than production from leaf litter (Figures 2–4, Table 4). However, if we make the same comparisons with *live* fine roots, DOC_{tps} production from leaf litter was 3.5 times greater than production from *live* fine roots, and DON_{tps} production from leaf litter was similar to production from *live* fine roots (except in the 77-year-old ecosystem, see Table 4). In contrast to DOC_{tps}, DOP_{tps} production from *live* fine roots was 1.2 times greater than production from leaf litter.

DOM_{tps} content from leaf litter was significantly greater than that from recently senesced fine roots for DOC_{tps} and DON_{tps}, but it was significantly lower than roots for DOP_{tps} (Tables 2 and 4). In comparison to DOM_{tps} content from *live* fine roots, we found that DOM_{tps} content from leaf litter was significantly greater for DOC_{tps}, but it was significantly lower for DON_{tps} and DOP_{tps}. Percent extractable DOM_{tps} comparisons between leaf and root categories were generally similar to comparisons of DOM_{tps} contents, except in the case of DON_{tps} content where recently senesced differed from live fine roots (see Tables 2, 3, and 4).

Finally, in comparing recently senesced fine roots to live fine roots, we found that DOC_{tps}, DON_{tps}, and DOP_{tps} contents were significantly higher in live roots (ANOVAs, $P < 0.001$, $P < 0.001$, $P = 0.031$, respectively). In the case of DON_{tps} content, recently senesced and live fine roots were not different in the youngest 77-year-old ecosystem (interaction term, $P = 0.01$). And, percent extractable DOC_{tps} (ANOVA, $P < 0.001$) and DON_{tps} (ANOVA, $P < 0.001$) in live fine roots was significantly greater than that in recently senesced fine roots, but similar for DOP_{tps} (ANOVA, $P = 0.11$).

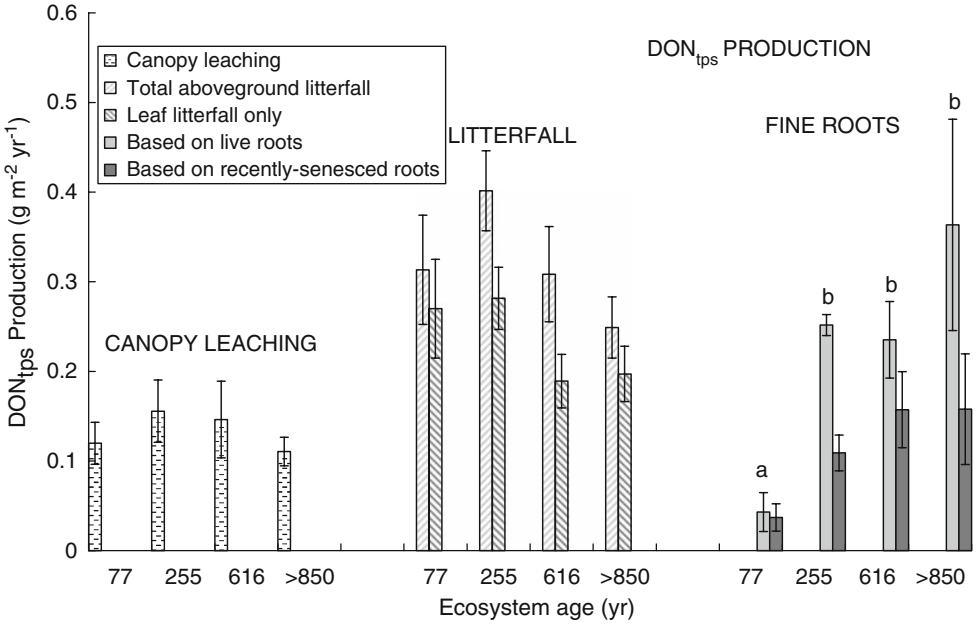

Figure 3. DON_{tps} production from canopy leaching, total aboveground litterfall, leaf litterfall only, live fine roots, and recently senesced fine roots (means ± SE in g m^{-2} y^{-1}) across an ecosystem chronosequence. Canopy leaching is throughfall minus open-area precipitation inputs. Each bar represents the average of five (or six) replicate plots. Effect of ecosystem age is as follows: canopy leaching ($P = 0.72$), total aboveground litterfall ($P = 0.19$), leaf litterfall only ($P = 0.20$), live fine roots ($P = 0.002$), and recently senesced fine roots ($P = 0.06$), based on separate one-way ANOVAs (on square-root transformed data). Means with different letters are significantly different (separate Tukey's HSD tests, $P < 0.05$) compared within each source. Two-way ANOVAs indicate that DON_{tps} production from leaf litter is significantly greater than production from recently senesced fine roots ($P < 0.001$) but not significantly different from production from live fine roots ($P = 0.27$).

Influence of Biomass Production versus Solubility of Litter on DOM_{tps} Production Across Ecosystem Chronosequence

Leaf litterfall, soluble contents, and DOM_{tps} production were separated by species, so we were able to explore the effect of species changes on variation in DOM_{tps} production from leaf litter across the chronosequence. Because DOM_{tps} contents of individual leaf species did not change significantly across the chronosequence, in most cases (Table 2), changes in soluble contents of individual species were likely to have little effect on changes in DOM_{tps} production. However, the species composition of leaf litterfall changed from predominantly *P. ponderosa* in the 77-year-old ecosystem to a mixture of conifer and one oak species in the older ecosystems (Table 1). Examining DOC_{tps} content of leaf litter (Table 2), for example, one can see that *P. ponderosa* leaf litter appeared to be lower than all of the other species. Despite this shift in species composition and the lower DOC_{tps} content of *P. ponderosa* leaf litter, we found that only 16% of the variability in DOC_{tps} production from leaf litterfall was due to changes in DOC_{tps} content, whereas the remainder (84%) was due to changes in leaf litterfall *biomass* production. The relative contribution of variability in biomass production versus DOM_{tps} content of litter in the calculation of DOM_{tps} production was determined using linear regression with DOM_{tps} production as the dependent variable and biomass production as the independent variable (leaf litterfall: $r^2 = 0.840$ for DOC_{tps}). Variation in DON_{tps} production from leaf litter was also largely a function of changes in leaf litterfall biomass production ($r^2 = 0.809$). In contrast to DOC_{tps} and DON_{tps}, DOP_{tps} production from leaf litter could not be explained by changes in biomass production ($r^2 = 0.086$), and was therefore strongly affected by variation in DOP_{tps} content of litter.

We did not separate other litter types (for example, woody) by species, but we assumed that these litter categories may vary in solubility with changes in aboveground species composition, allowing for a similar assessment of the importance of biomass production on the calculation of DOM_{tps} production. For DOC_{tps} and DON_{tps} production from total aboveground litterfall, over 80% of the variability was explained by changes in biomass

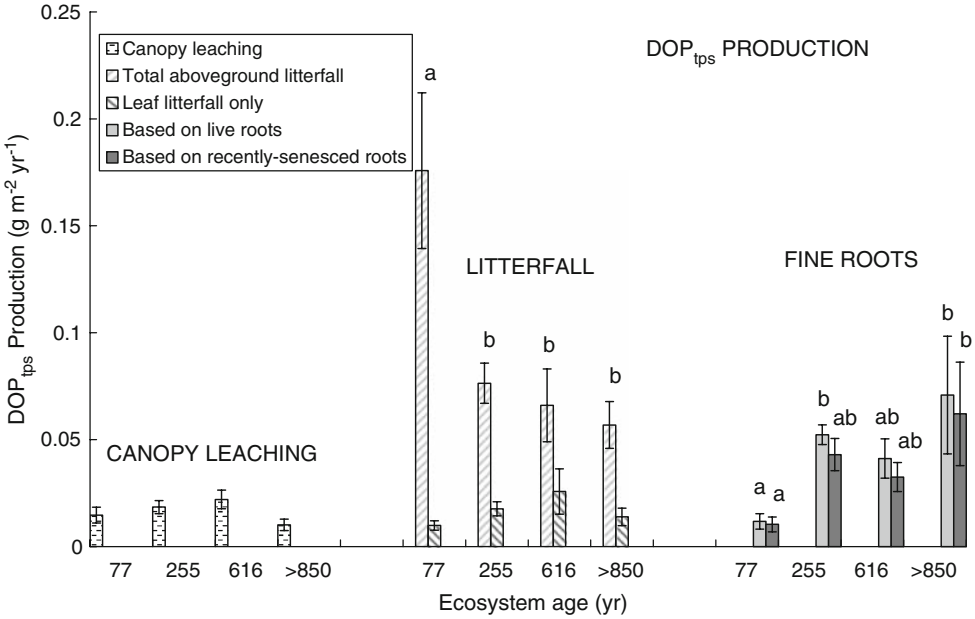

Figure 4. DOP$_{tps}$ production from canopy leaching, total aboveground litterfall, leaf litterfall only, live fine roots, and recently senesced fine roots (means ± SE in g m^{-2} y^{-1}) across an ecosystem chronosequence. Canopy leaching is throughfall minus open-area precipitation inputs. Each bar represents the average of five (or six) replicate plots. Effect of ecosystem age is as follows: canopy leaching (P = 0.13), total aboveground litterfall (P = 0.003), leaf litterfall only (P = 0.26), live fine roots (P = 0.01), and recently senesced fine roots (P = 0.01), based on separate one-way ANOVAs (on square-root transformed data). Means with different letters are significantly different (separate Tukey's HSD tests, $P < 0.05$) compared within each source. Two-way ANOVAs indicate that DOP$_{tps}$ production from leaf litter is significantly lower than both production from recently senesced fine roots (P = 0.005) and live fine roots (P = 0.001).

production (r^2 = 0.862 for DOC$_{tps}$, and r^2 = 0.827 for DON$_{tps}$), despite some significant differences in DOC$_{tps}$ and DON$_{tps}$ contents of woody and reproductive litter among ecosystem ages (Table 2). The pattern of DOP$_{tps}$ production from total aboveground litterfall was heavily influenced by the high DOP$_{tps}$ content of the reproductive litter of the dominant species *P. ponderosa* in the youngest ecosystem (Table 2, Figure 4), and thus there was no relationship to biomass production (r^2 = 0.102). For DOM$_{tps}$ production from fine roots, 69% to 91% of the variability was explained by changes in root biomass production across the chronosequence (r^2 = 0.755 for DOC$_{tps}$, r^2 = 0.858 for DON$_{tps}$, and r^2 = 0.817 for DOP$_{tps}$ for recently senesced fine roots; and r^2 = 0.907 for DOC$_{tps}$, r^2 = 0.689 for DON$_{tps}$, and r^2 = 0.863 for DOP$_{tps}$ for live fine roots), despite some significant differences in DOC$_{tps}$, DON$_{tps}$, and DOP$_{tps}$ contents of fine roots among ecosystem ages (Table 2).

In general, variability of DOC$_{tps}$ and DON$_{tps}$ contents of litter were much smaller than that of DOP$_{tps}$, explaining the better relationship between DOC$_{tps}$ and DON$_{tps}$ production and biomass production. In contrast to aboveground DOP$_{tps}$ production, belowground DOP$_{tps}$ production could be explained by changes in biomass production, likely due to much lower variation in DOP$_{tps}$ contents of fine roots. In summary, DOC$_{tps}$ and DON$_{tps}$ production were predominantly driven by changes in biomass production during ecosystem development, and changes in litter solubility (that is, DOM$_{tps}$ content of litter) had a smaller effect.

Discussion

Magnitude of DOM$_{tps}$ Production from Root Litter—Comparison to Other Sources

DOM$_{tps}$ production from root litter was a very important source of DOM$_{tps}$ in the Mt. Shasta mudflow ecosystems, in some cases comparable to production from leaf litter for DON$_{tps}$ and larger than production from leaf litter for DOP$_{tps}$ (Table 4). We had hypothesized that DOM$_{tps}$ production from freshly senesced fine root litter would be greater than DOM$_{tps}$ production from freshly

Table 1. Litter Production by Litter Category and Ecosystem Age*

Litter category	Litter production (g m^{-2} y^{-1})				
	Ecosystem age (year)				ANOVA
	77-year-old	255-year-old	616-year-old	>850-year-old	
P. ponderosa (g m^{-2} y^{-1})†	259 ± 36	76 ± 34	4.4 ± 3.1	39 ± 28	$P < 0.001$‡
(%)	(66)	(16)	(1.2)	(12)	
C. decurrens (g m^{-2} y^{1})†	1.93 ± 0.77	99 ± 29	43.5 ± 5.0	98 ± 37	$P < 0.001$
(%)	(0.5)	(20)	(12)	(31)	
A. concolor (g m^{-2} y^{-1})†	0.41 ± 0.21	126 ± 25	52 ± 30	74 ± 23	$P < 0.001$
(%)	(0.1)	(26)	(14)	(23)	
P. menziesii (g m^{-2} y^{-1})†	8.3 ± 7.1	0.68 ± 0.54	58 ± 35	0.29 ± 0.18	$P = 0.06$‡
(%)	(2.1)	(0.1)	(16)	(0.1)	
Q. kelloggii (g m^{-2} y^{-1})†	0.77 ± 0.44	4.5 ± 2.1	38 ± 13	13 ± 12	$P = 0.01$
(%)	(0.2)	(0.9)	(11)	(4.0)	
P. lambertiana (g m^{-2} y^{-1})†	15.3 ± 5.2	0.86 ± 0.32	12.3 ± 7.5	0.01 ± 0.01	$P = 0.01$‡
(%)	(3.9)	(0.2)	(3.4)	(<0.1)	
Woody (g m^{-2} y^{-1})	46 ± 18	115 ± 13	91 ± 25	51.6 ± 8.7	$P = 0.01$
(%)	(12)	(24)	(25)	(16)	
Reproductive (g m^{-2} y^{-1})	57 ± 12	53 ± 10	46 ± 17	39.3 ± 5.1	$P = 0.72$
(%)	(14)	(11)	(13)	(12)	
Unknown (g m^{-2} y^{-1})	6.8 ± 1.1	12.1 ± 1.9	12.4 ± 2.4	5.41 ± 0.84	$P = 0.01$
(%)	(1.7)	(2.5)	(3.5)	(1.7)	
Total leaf litterfall (g m^{-2} y^{-1})§	286 ± 33	308 ± 27	208 ± 36	223 ± 28	$P = 0.10$
(%)	(72)	(63)	(58)	(70)	
Total aboveground production (g m^{-2} y^{-1})§	395 ± 53	487 ± 44	358 ± 62	320 ± 31	$P = 0.11$
Total fine root production (g m^{-2} y^{-1})§	44 ± 13	168 ± 21	190 ± 34	236 ± 65	$P = 0.001$

*Values are mean ± SE (g m^{-2} y^{-1}). Each aboveground category is also shown as a percentage of the total aboveground production. Mass is reported on an oven-dry basis for aboveground production and on an oven-dry, ash-free basis for root production. Each mean represents the average of five to six replicate plots, and each plot average is based on two to three subsamples. ANOVAs show significance of differences among ecosystem ages. For the ANOVAs, category data were transformed by $\log_{10}(X + 1)$, fine root production data were ln-transformed, and leaf and total aboveground production data were not transformed.

†Leaf litter was separated by species.

§Data cited from Uselman and others (2007a).

‡Welch F-ratio.

senesced leaf litter, but our data showed that this varied by element. Leaf litter has long been recognized as an important source of DOC production (for example, Nykvist 1963; McDowell and Fisher 1976; Qualls and others 1991), especially for its role in soil horizon development and organic matter accumulation. In this study, leaf litter was a greater source of DOC_{tps} than root litter, both in terms of solubility of the litter (Table 2) and ecosystem production (Figure 2). Of total ecosystem DOC_{tps} production, production from leaf litter accounted for 55–61% (Table 5).

DOM_{tps} production from root litter (in g m^{-2} y^{-1}) has never been directly measured, or it has only been speculated upon as a source of DOM production in ecosystems, so we are unable to compare our measurements with other studies. However, Yano and others (2005) found that the water-extractable DOC and DON contents (mg g^{-1}) of Douglas fir seedling roots were greater than that of Douglas fir needle litter (defined as O_i horizon freshly fallen intact needles with minimal decay), and they suggested that root litter may be an important source of DOC and DON in forested ecosystems.

In comparison to DOM_{tps} production from root and leaf litter, canopy leaching was the smallest source of DOM in this study. It accounted for at most 16% of total DOC_{tps}, 24% of total DON_{tps}, and 12% of total DOP_{tps} production (Figures 2–4, Table 5). These results are consistent with results from Coweeta Hydrologic Laboratory, a temperate deciduous forest in North Carolina, USA (Qualls and others 1991), where DOC from throughfall (which includes inputs from canopy leaching and above-canopy precipitation) was less than one-third the input from fresh leaf litter. In addition, our values of canopy leaching fluxes were within the ranges of throughfall values reported in a

Table 2. Total Potentially Soluble Organic C/N/P Content of Litter*

Litter category	Ecosystem age (year)				ANOVA
	77-year-old	255-year-old	616-year-old	>850-year-old	
	DOC_{tps} originating from litter (mg DOC_{tps} g^{-1} dry weight)				
Recently senesced roots	26.0 ± 3.3	27.1 ± 1.0	21.9 ± 0.9	33.7 ± 2.1	$P = 0.008$
Live roots	48.7 ± 10.5	65.7 ± 11.7	47.5 ± 2.7	81.8 ± 7.7	$P = 0.046$
Leaf litter					
P. ponderosa	104.7 ± 4.9	109.1 ± 3.5	84.8 ± 23.7	112.6 ± 7.7	$P = 0.74^{\dagger}$
C. decurrens	NA	132.7 ± 1.7	122.9 ± 4.2	129.5 ± 7.3	$P = 0.20^{\dagger}$
A. concolor	NA	146.8 ± 9.5	150.2 ± 17.2	143.1 ± 10.7	$P = 0.92$
P. menziesii	NA	NA	122.2 ± 15.1	NA	
Q. kelloggii	NA	NA	121.5 ± 6.6	133.5 ± 43.6	$P = 0.83^{\dagger}$
P. lambertiana	NA	NA	NA	NA	
Woody	32.7 ± 3.5	37.2 ± 2.6	45.5 ± 6.7	36.6 ± 4.8	$P = 0.58$
Reproductive	25.0 ± 2.3	71.7 ± 3.4	84.0 ± 16.4	75.6 ± 2.4	$P < 0.001^{\dagger}$
Unknown	NA	NA	NA	NA	
	DON_{tps} originating from litter (mg DON_{tps} g^{-1} dry weight)				
Recently senesced roots	0.767 ± 0.101	0.679 ± 0.122	0.783 ± 0.108	0.695 ± 0.243	$P = 0.95$
Live roots	0.813 ± 0.184	1.576 ± 0.174	1.260 ± 0.202	1.530 ± 0.195	$P = 0.043$
Leaf litter					
P. ponderosa	0.916 ± 0.083	1.059 ± 0.028	0.872 ± 0.189	1.195 ± 0.053	$P = 0.062$
C. decurrens	NA	0.841 ± 0.041	0.853 ± 0.037	0.800 ± 0.058	$P = 0.72$
A. concolor	NA	0.817 ± 0.059	0.855 ± 0.184	0.729 ± 0.079	$P = 0.65$
P. menziesii	NA	NA	0.837 ± 0.063	NA	
Q. kelloggii	NA	NA	1.294 ± 0.082	1.771 ± 0.186	$P = 0.047$
P. lambertiana	NA	NA	NA	NA	
Woody	0.369 ± 0.114	0.516 ± 0.039	0.373 ± 0.091	0.184 ± 0.049	$P = 0.046$
Reproductive	0.388 ± 0.056	1.012 ± 0.061	1.384 ± 0.262	0.962 ± 0.051	$P < 0.001^{\dagger}$
Unknown	NA	NA	NA	NA	
	DOP_{tps} originating from litter (mg DOP_{tps} g^{-1} dry weight)				
Recently senesced roots	0.232 ± 0.023	0.250 ± 0.015	0.168 ± 0.011	0.249 ± 0.034	$P = 0.013^{\dagger}$
Live roots	0.252 ± 0.018	0.319 ± 0.020	0.223 ± 0.052	0.280 ± 0.028	$P = 0.23$
Leaf litter					
P. ponderosa	0.032 ± 0.011	0.052 ± 0.008	0.052 ± 0.027	0.065 ± 0.017	$P = 0.35$
C. decurrens	NA	0.073 ± 0.029	0.030 ± 0.005	0.037 ± 0.007	$P = 0.35^{\dagger}$
A. concolor	NA	0.049 ± 0.008	0.067 ± 0.026	0.088 ± 0.008	$P = 0.086$
P. menziesii	NA	NA	0.206 ± 0.042	NA	
Q. kelloggii	NA	NA	0.137 ± 0.023	0.046 ± 0.021	$P = 0.066$
P. lambertiana	NA	NA	NA	NA	
Woody	0.035 ± 0.006	0.042 ± 0.013	0.079 ± 0.012	0.064 ± 0.020	$P = 0.046^{\dagger}$
Reproductive	2.912 ± 0.216	1.018 ± 0.117	1.127 ± 0.444	0.984 ± 0.059	$P < 0.001$
Unknown	NA	NA	NA	NA	

**Values are mean ± SE (mg DOC_{tps}, DON_{tps}, or DOP_{tps} g^{-1} dry weight). Mass is reported on an oven-dry basis for aboveground litter production, whereas it is reported on an oven-dry, ash-free basis for root production. Each mean represents the average of five to six replicate plots, except in cases where there was insufficient material for analysis. ANOVAs show significance of differences among ecosystem ages. Note: NA = not analyzed due to insufficient mass for extraction.*

†Welch F-ratio.

review of DOC and DON fluxes in temperate forests (Michalzik and others 2001).

In estimating DOM_{tps} production from fine roots, we measured production from freshly senesced fine roots and production from live fine roots. We did this because roots do not die in an obvious manner as do leaves, by forming an abscission layer (eventually falling off the plant); rather, natural root senescence is a transitional non-abrupt process. Although Nambiar (1987) found that N and P were not retranslocated from *Pinus radiata* fine roots during senescence, the issue of retrans-

Table 3. Total Potentially Soluble Organic C/N/P as Percentage of Total C/N/P in Litter*

Litter category	Ecosystem age (year)				ANOVA
	77-year-old	255-year-old	616-year-old	>850-year-old	
	Percent extractable DOC_{tps} (DOC_{tps} as % of total C)				
Recently senesced roots	5.7 ± 0.8	6.2 ± 0.3	5.4 ± 0.2	7.7 ± 0.4	$P = 0.017$
Live roots	12.8 ± 2.3	16.2 ± 2.6	12.8 ± 1.1	18.8 ± 1.4	$P = 0.12$
Leaf litter					
P. ponderosa	20.7 ± 0.9	21.4 ± 0.6	16.5 ± 4.4	21.8 ± 1.4	$P = 0.78^{\dagger}$
C. decurrens	NA	26.2 ± 0.4	24.6 ± 0.8	25.5 ± 1.4	$P = 0.29^{\dagger}$
A. concolor	NA	29.4 ± 1.9	29.6 ± 3.5	28.5 ± 2.1	$P = 0.94$
P. menziesii	NA	NA	24.7 ± 2.5	NA	
Q. kelloggii	NA	NA	25.0 ± 1.3	27.1 ± 9.1	$P = 0.85^{\dagger}$
P. lambertiana	NA	NA	NA	NA	
Woody	6.4 ± 0.6	7.4 ± 0.5	9.0 ± 1.3	7.2 ± 0.9	$P = 0.22$
Reproductive	4.7 ± 0.4	13.4 ± 0.6	16.1 ± 3.5	14.0 ± 0.4	$P < 0.001^{\dagger}$
Unknown	NA	NA	NA	NA	
	Percent extractable DON_{tps} (DON_{tps} as % of total N)				
Recently senesced roots	6.6 ± 0.8	6.1 ± 1.0	7.2 ± 0.9	5.6 ± 1.6	$P = 0.79$
Live roots	10.5 ± 1.9	14.5 ± 1.1	11.8 ± 1.2	13.1 ± 1.3	$P = 0.26$
Leaf litter					
P. ponderosa	16.5 ± 0.4	20.9 ± 1.2	17.0 ± 8.5	22.5 ± 4.7	$P = 0.18^{\dagger}$
C. decurrens	NA	21.2 ± 2.5	21.5 ± 1.9	22.7 ± 3.0	$P = 0.91$
A. concolor	NA	16.7 ± 1.3	18.7 ± 4.6	14.0 ± 1.2	$P = 0.36^{\dagger}$
P. menziesii	NA	NA	22.3 ± 3.0	NA	
Q. kelloggii	NA	NA	18.1 ± 0.5	25.3 ± 7.3	$P = 0.50^{\dagger}$
P. lambertiana	NA	NA	NA	NA	
Woody	7.4 ± 2.1	14.0 ± 1.6	6.6 ± 2.0	4.4 ± 1.0	$P = 0.005$
Reproductive	1.8 ± 0.3	10.1 ± 0.4	15.9 ± 5.1	10.8 ± 0.5	$P < 0.001^{\dagger}$
Unknown	NA	NA	NA	NA	
	Percent extractable DOP_{tps} (DOP_{tps} as % of total P)				
Recently senesced roots	17.7 ± 1.8	21.8 ± 1.1	NA	14.7 ± 2.0	$P = 0.035$
Live roots	16.4 ± 1.1	18.5 ± 1.2	13.7 ± 1.8	13.9 ± 1.8	$P = 0.12$
Leaf litter					
P. ponderosa	4.6 ± 1.6	7.5 ± 1.0	7.7 ± 4.1	8.8 ± 2.1	$P = 0.35$
C. decurrens	NA	13.1 ± 3.4	6.7 ± 1.1	8.2 ± 0.6	$P = 0.24^{\dagger}$
A. concolor	NA	7.6 ± 1.6	8.3 ± 2.8	15.2 ± 1.7	$P = 0.026$
P. menziesii	NA	NA	12.9 ± 2.5	NA	
Q. kelloggii	NA	NA	10.2 ± 1.9	3.0 ± 1.3	$P = 0.075$
P. lambertiana	NA	NA	NA	NA	
Woody	11.6 ± 2.0	9.2 ± 2.4	11.0 ± 1.4	16.6 ± 5.5	$P = 0.41$
Reproductive	71.8 ± 3.2	58.8 ± 3.7	54.7 ± 13.7	67.8 ± 5.1	$P = 0.37$
Unknown	NA	NA	NA	NA	

**Values are mean ± SE (DOC_{tps}, DON_{tps}, or DOP_{tps} as percentages of total C, N, or P, respectively). Each mean represents the average of five to six replicate plots, except where there was insufficient material for analysis. ANOVAs show significance of differences among ecosystem ages. Note: NA = not analyzed due to insufficient mass for extraction.*
†Welch F-ratio.

location in fine roots is still unclear (Gordon and Jackson 2000). Overall, our estimate of DOM_{tps} production from live fine roots was significantly greater than production from recently senesced roots. By also measuring DOM_{tps} production from live fine roots, we were able to set an upper limit to our estimate of DOM_{tps} production from recently senesced fine roots, so it is likely that DOM_{tps} production from fine root litter falls between these two estimates.

Because root exudation has received a great deal of interest in the past decade as a potentially important belowground C flux, we estimated the relative importance of DOC_{tps} production from root

Table 4. Summary Comparisons of DOM_{tps} Originating from Root versus Leaf Litter[§]

Variable	Comparisons of root versus leaf litter		
	DOC_{tps}	DON_{tps}	DOP_{tps}
Total DOM_{tps} production (g m^{-2} y^{-1})	Root < Leaf***	Recently senesced root < Leaf*** Live root = Leaf[†]	Leaf < Root**
Soluble DOM_{tps} content (mg g^{-1} dry weight)	Root < Leaf***	Recently senesced root < Leaf* Leaf < Live root**	Leaf < Root***
% Extractable DOM_{tps} (as % of total C/N/P)	Root < Leaf***	Root < Leaf***	Leaf < Root***

[§]Comparisons of main effects of source (root versus leaf) based on split-plot ANOVA results, with the following significance levels:
**P < 0.05.*
***P < 0.01.*
****P < 0.001.*
[†]In the case of total DON_{tps}, production from live fine roots and leaf litter were not significantly different overall (ANOVA, P = 0.27). However, a significant interaction with ecosystem age (P < 0.05) showed that production from live fine roots was less than production from leaf litter in the youngest 77-year-old ecosystem.

litter using our study compared to DOC production from root exudation using literature values. For comparative purposes, we calculated DOC_{tps} production from root litter as a fraction of total NPP in the >850-year-old ecosystem. We used (1) our measurements of DOC_{tps} production from fine roots (based on both recently senesced and live fine roots) and (2) an estimate of total NPP. To estimate total NPP in the >850-year-old ecosystem, we used our measurements of litterfall and fine root production (Uselman and others 2007a) and estimated woody increment (stem + coarse roots) from a C budget study of old-growth Ponderosa pine at the Metolius AmeriFlux site in central Oregon (Law and others 2001). At their old-growth site, the ratio of fine litter production (litterfall + fine root) to total NPP was 0.86, with the remainder being woody increment. We calculated total NPP at our site by multiplying our measurement of fine litter production by the inverse of this ratio, which resulted in total NPP of 643–782 g m^{-2} y^{-1}, or 322–391 g C m^{-2} y^{-1} (based on 50% C). Using these NPP values, we estimated that DOC_{tps} production from root litter accounted for 2–6% of total NPP in the >850-year-old ecosystem. In a review of rhizodeposition, Jones and others (2004) stated that ''it is likely that a true estimate of root exudation [is] 2–4% of net fixed C,'' and other studies have found a similar % of total NPP in trees (Smith 1976; Uselman and others 2000). Thus, DOC_{tps} production from root litter is comparable in magnitude to DOC production from live root exudation.

Furthermore, using this estimate of NPP, total DOC_{tps} comprises a large component of total NPP, approximately 12–18% of the C in total NPP in the >850-year-old ecosystem. Such a large component of the NPP being potentially soluble in water could profoundly affect the potential for translocation and storage in mineral soil, leaching from the ecosystem, and availability for microbial uptake.

Patterns in DOM_{tps} Production Across Ecosystem Chronosequence—Implications for Ecosystem Nutrient Storage

Our study showed that total DOM_{tps} production increased early in succession from the 77- to the 255-year-old ecosystem (for DOC_{tps} and DON_{tps}), as we had hypothesized (Figure 1). In addition, DOM_{tps} production should have increased from zero at the initiation of primary succession. But, after the 255-year-old ecosystem, DOM_{tps} did not continue to increase across the chronosequence.

Table 5. DOM_{tps} Production by Source, as Percentage of Total DOM_{tps} Production*

DOM_{tps} source/total	DOC_{tps} (%)	DON_{tps} (%)	DOP_{tps} (%)
Canopy leaching	16–15	24–20	12–12
Aboveground litterfall	75–67	57–49	61–58
Leaf litterfall only	61–55	43–37	12–12
Fine roots	11–17	19–30	27–30

Percentage is shown as a range: the first number uses total DOM_{tps} calculated with extractions of recently senesced roots, and the second number uses total DOM_{tps} calculated with extractions of live roots.

Total DOP_{tps} production did not show a significant trend with age.

Patterns in DOM_{tps} production across the ecosystem chronosequence became clearer when we examined individual sources separately (Figures 2–4). For DOM_{tps} production from fine roots, we found that DOC_{tps}, DON_{tps}, and DOP_{tps} production appeared to reach a maximum by the 255-year-old ecosystem. In addition, DOC_{tps} and DON_{tps} production from aboveground litterfall, and from leaf litter only, also appeared to be highest in the 255-year-old ecosystem.

Although DOP_{tps} production from leaf litterfall did not differ significantly among ecosystem ages, DOP_{tps} production from *all* aboveground litterfall had a unique pattern where the youngest 77-year-old ecosystem was significantly higher than the older ecosystems (Figure 4). This unique pattern was caused by the high DOP_{tps} content of the reproductive category (Table 2), resulting from the greater abundance of cones of the early successional species *P. ponderosa* in the youngest ecosystem. In general, we found that DOC_{tps} and DON_{tps} behave relatively similarly, whereas DOP_{tps} behaves differently.

In a companion study, we found that the relative contribution of fine roots to total fine detrital production increased during ecosystem development (Uselman and others 2007a), leading us to hypothesize in this study that the relative contribution of belowground DOM_{tps} production to total fine detrital DOM_{tps} production (from roots + leaf litter) would also increase across the chronosequence. Because DOC_{tps} and DON_{tps} production were largely a function of increases in biomass production, we found that the relative importance of root litter for total fine detrital DOC_{tps} and DON_{tps} production generally increased significantly across the ecosystem chronosequence, as we had predicted (Table 6). In the case of DOP_{tps}, the differences among ecosystem ages were of borderline significance.

DOM production may be important in the development and deepening distribution of SOM during ecosystem development. Furthermore, DON that is produced and incorporated into SOM may be an important pathway for long-term N storage

Table 6. Contribution of Belowground to Total Fine Detrital DOM_{tps} Production* Across Ecosystem Chronosequence†

	Root DOM_{tps}/Fine detrital DOM_{tps} (%)				
Element	Ecosystem age (year)				ANOVA
	77-year-old	255-year-old	616-year-old	>850-year-old	
Using recently senesced roots					
DOC_{tps}	4 ± 2% (a)	10 ± 1% (ab)	15 ± 3% (b)	22 ± 5% (b)	$P = 0.003$
DON_{tps}	13 ± 5% (a)	26 ± 4% (ab)	43 ± 6% (b)	40 ± 9% (b)	$P = 0.006$
DOP_{tps}	48 ± 10% (a)	69 ± 5% (ab)	59 ± 4% (ab)	77 ± 7% (b)	$P = 0.058$
Using live roots					
DOC_{tps}	9 ± 5% (a)	20 ± 2% (ab)	27 ± 5% (b)	38 ± 6% (b)	$P = 0.001$
DON_{tps}	14 ± 6% (a)	46 ± 4% (b)	54 ± 7% (b)	61 ± 6% (b)	$P < 0.001$
DOP_{tps}	51 ± 12%	74 ± 3%	64 ± 7%	79 ± 6%	$P = 0.073$

*Total fine detrital DOM_{tps} production is defined as DOM_{tps} production from fine roots and leaf litter.
†Values are mean ± SE, shown as percentage. Two separate calculations were done for this analysis, (1) using recently senesced root extractions, and (2) using live root extractions. Individual ANOVAs and Tukey's HSD tests (different lowercase letters, $P < 0.05$) show significance of difference among ecosystem ages (proportion data transformed by arcsine ($\sqrt{p}$)).

(McDowell 2003). Patterns of SOM accumulation, both in total accumulation in the entire soil profile and in depth distribution, have been observed in primary succession studies in general (Schlesinger 1991), including Mt. Shasta (Dickson and Crocker 1953b; Sollins and others 1983; Lilienfein and others 2003). In a synthesis of past data at the Mt. Shasta site, we found that soil C and N accumulation increased linearly with ecosystem age, with a rate of 13.9 g m^{-2} y^{-1} for C, and the distribution of C and N deepened (Lilienfein and others 2003). The rate of DOC_{tps} production in all ecosystem ages was considerably greater than the rate of accumulation of soil organic C across the chronosequence (Figure 1). On average, DOC_{tps} production was 3–5 times greater than soil organic C accumulation, thus the soluble component of detrital production was more than enough to account for the rate of soil organic C accumulation. However, solid sources also contribute to soil organic C accumulation. Since it is in solution, DOM can be translocated in soil solution to greater depths, where it can potentially be adsorbed–although it may also be respired or otherwise lost from the ecosystem. Although production of DOM_{tps} generally increased from the inception of ecosystem development, at least until the 255-year-old ecosystem (except DOP_{tps}), soils also developed an increasing adsorption capacity for DOM, both in total and with depth, mainly as a result of the formation of allophane (Lilienfein and others 2003, 2004a, b). Therefore, DOM produced in the forest floor or surface soil can move into the relatively allophane-rich B horizon, where it has been shown to adsorb to the soil, potentially contributing to SOM accumulation at depth (Uselman and others 2007b). Sollins and others (1983) found that dense (or heavy) fraction-SOM, composed of organic matter ''adsorbed on mineral surfaces and occluded within organo-mineral aggregates,'' increased consistently with ecosystem age at the Mt. Shasta site. Their results suggest that SOM adsorbed onto mineral surfaces originated from DOM, which is also consistent with our results. Qualls and Bridgham (2005) also found that a large fraction of $DO^{14}C$ originating from aboveground litter, and incubated in soil from our site, has a half-decay time of 1.6 years, further illustrating the potential for DOM to contribute to the accumulation of SOM.

During ecosystem development, production of DOM_{tps} (or *input* of DOM) from root litter may be particularly important in the development of more deeply distributed SOM. Location of origin may play a role in determining the fate of DOM from different sources. In contrast to DOM_{tps} from leaf litter, which is produced in the forest floor, DOM_{tps} originating from fine root litter is produced mainly in the upper 30 cm of mineral soil in this ecosystem (Uselman and others 2007a). Because it is directly deposited in the mineral soil, it may be more likely to be adsorbed and retained by the ecosystem. We suggest that fine roots may play an increasingly fundamental role in the accumulation of SOM during ecosystem development at the Mt. Shasta site because (1) fine roots become more deeply distributed during ecosystem development (Uselman and others 2007a), and (2) fine roots contribute an increasing proportion of total fine detrital DOM_{tps} production during ecosystem development. DOM_{tps} originating from fine roots may also contribute to deep leaching, especially for DOM_{tps} originating from roots present deeper in the soil profile. Deep leaching should be more likely to occur in the youngest soil of the Mt. Shasta chronosequence, where the adsorption capacity for DOM is low both in total and at depth (Lilienfein and others 2004a), as we have demonstrated in a companion laboratory column study (Uselman and others 2007b).

In general, DOM may both contribute to SOM accumulation, and it may also be a vehicle for loss of organic matter through leaching (that is, export as a SOM sink, Perakis and Hedin 2002). The controls on DOM as a source and a sink of SOM are largely NPP, soil chemical, physical and biological properties, and hydrologic flow (Qualls 2000). The balance of these factors shifts as an ecosystem ages. Early in primary succession, retention of DOM within the ecosystem may largely be dominated by changes in NPP, whereas late in ecosystem development, retention may be controlled by soil development. At the Mt. Shasta site, we not only found that DOM_{tps} production generally increased during early stages of ecosystem development, mainly due to increases in biomass production, but we also found increased adsorption capacity of soil to retain DOM (Lilienfein and others 2004a, b). Increased adsorption capacity may help, *in part*, to explain how it is possible that SOM could continue to increase linearly over the chronosequence when DOM_{tps} inputs appear to follow more of an asymptotic pattern. We suggest that whereas DOM_{tps} production may be more important in controlling DOM dynamics in this ecosystem early in succession, mineral soil adsorption capacity appears to regulate DOM retention later in ecosystem development.

Influence of Biomass Production versus Solubility of Litter on DOM_{tps} Production Across Ecosystem Chronosequence

We had hypothesized that changes in species composition would have an effect on DOM_{tps} production across the ecosystem chronosequence. Changes in species can influence soil properties and processes (Pohlman and McColl 1988; Binkley 1995), and these changes are thought to be largely mediated through differences in the quantity or quality of plant tissue and detritus. In this study, we found that DOC_{tps} and DON_{tps} production were predominantly driven by changes in biomass production during ecosystem development, and changes in litter solubility (that is, DOM_{tps} content of litter) had a smaller effect. If our results hold true for other ecosystems, then in a broader ecological context, increases in primary production during ecosystem development are the primary driver of DOM_{tps} production, not changes in the solubility of different species. In the case of the ecosystem chronosequence at the Mt. Shasta site, *P. ponderosa* dominance in the youngest ecosystem is replaced by a mixed-conifer forest in the older ecosystems. We believe that it would be very interesting to test whether the patterns observed at the Mt. Shasta site would be observed in other ecosystem chronosequences. For example, would changes in solubility play a larger role in DOM_{tps} production during ecosystem development in a forest progressing from predominantly coniferous to broadleaf deciduous species, or in the case of invasion by one very different species?

Although belowground DOP_{tps} production was also predominantly driven by biomass production, this was not the case for aboveground DOP_{tps} production. In this case, an individual species did determine the variation in aboveground DOP_{tps} production, the result of the greater abundance of cones of the early successional species *P. ponderosa* in the youngest ecosystem (Tables 1 and 2).

Significance of Measuring Gross Rates of DOM Production

In this study, we aimed to measure the total content and production of water-soluble organic matter originating from primary production, because this production serves as a source of DOM for the ecosystem. This was the rationale for using methods to completely extract the water-soluble component of organic matter. Very few studies have estimated gross rates of DOM production from freshly fallen leaf litter (or other aboveground litter). Because other studies have not directly measured DOM_{tps} production from belowground sources, we are limited to a comparison of aboveground sources. For example, in the 255-year-old ecosystem at the Mt. Shasta site, DOM_{tps} production that was deposited on the forest floor (that is, production from aboveground litterfall and throughfall only) was 60.1, 0.591, and 0.100 g m^{-2} y^{-1} for DOC_{tps}, DON_{tps}, and DOP_{tps}. In comparison, gross production from freshly fallen foliar litterfall, throughfall, and stemflow was 59.5, 0.704, and 0.105 g m^{-2} y^{-1} for DOC, DON, and DOP in a temperate deciduous forest at Coweeta Hydrologic Laboratory (from calculations in Qualls and others 2002). Stemflow was a very minor contribution to total aboveground DOM production at Coweeta (Qualls and others 1991). In a similar calculation using data in McDowell and Likens (1988), the gross aboveground DOC production was 31.0 g m^{-2} y^{-1} in a northern hardwood forest at the Hubbard Brook Experimental Forest.

Differences between gross DOM production from aboveground litter and net fluxes from the forest floor illustrate the need to quantify gross rates of production separately from net rates, as identified by McDowell (2003). Measurement of DOM fluxes from the bottom of the forest floor does not represent gross DOM production because decomposition or sorption of DOM may occur. Using data from Qualls and others (1991) of measurements at Coweeta forest, we calculated that approximately 36% of the DOC that was deposited on the forest floor (as gross production from aboveground litterfall and throughfall) was not leached from the bottom of the forest floor and was thus either adsorbed or respired.

Our approach of dividing O.M. (that is, detritus) production into water-soluble and water-insoluble components does not *alone* allow determination of the eventual fate and transport of DOM. Assessment of the fate and transport of this potentially water-soluble material would require additional experiments such as assays of the biodegradability of DOM and tracer experiments (for example, Hagedorn and others 2004; McDowell and others 2006; Qualls and Bridgham 2005; Uselman and others 2007b). In a companion laboratory column study, 21.6% of the ^{14}C in ^{14}C-labeled leaf litter was either leached from the 50-cm soil columns or translocated into the mineral soil (Uselman and others 2007b). Additionally, 7.5% of the ^{14}C in ^{14}C-labeled root litter (located at 10 cm deep in the soil column) was either leached from the columns or translocated within the mineral soil. Furthermore, in another companion study using soils of

the Mt. Shasta chronosequence, in which the water-soluble and water-insoluble components of the ^{14}C-labeled leaf litter were separated, a greater percentage of the C was lost to respiration from the water-soluble (54.6%) versus insoluble (31.9%) components over 1 year (Qualls and Bridgham 2005). Cleveland and others (2006) found that additions of DOM leached from freshly fallen litter to soil stimulated profound shifts in microbial species composition and increased microbial respiration. These results show that portions of the soluble organic matter leached from litter can leach from the ecosystem, contribute to the accumulation of SOM, and serve as an important substrate for soil microbial respiration.

Rates of leaching and microbial utilization of DOM in the field will differ due to variation in abiotic factors (for example, precipitation, temperature, and soil type). In general, fresh litter and older organic matter may continue to leach substantial amounts of DOC for long periods of time, as suggested by the studies of Hagedorn and others (2004) and Fröberg and others (2007). The fact that numerous extractions were needed to completely desorb the DOM_{tps} in our study may help explain the very slow release or desorption of this material from the forest floor, perhaps persisting over years, and may also help explain the results of litter exclusion or labeling experiments (for example, Hagedorn and others 2004; Fröberg and others 2007) showing substantial release of DOM from the Oe/Oa horizon. Fröberg and others (2007) also attributed some of the removal of new DOC to resorption within the Oe/Oa horizon.

Conclusions

1. DOM_{tps} production from root litter was a very important source of DOM_{tps} in the Mt. Shasta mudflow ecosystems, in some cases comparable to production from leaf litter for DON_{tps} and larger than production from leaf litter for DOP_{tps}. Therefore, studies that do not measure DOM_{tps} production from roots could seriously underestimate DOM_{tps} production in forest ecosystems.
2. DOM_{tps} represents a substantial proportion of primary production, for example 12–18% of NPP in the case of C was DOC_{tps} in the >850-year-old ecosystem. Furthermore, we found that considerable proportions of the N and P in a variety of types of litter were water-soluble.
3. Across the ecosystem chronosequence, we found that total DOC_{tps} and DON_{tps} production increased early in succession from the 77- to the 255-year-old ecosystem. In contrast, the pattern of total DOP_{tps} production was unique. Generally, the relative importance of root litter for total fine detrital DOC_{tps} and DON_{tps} production increased significantly during ecosystem development.
4. During ecosystem development, DOC_{tps} and DON_{tps} production were predominantly driven by changes in biomass production, and changes in litter solubility due to changes in species composition had a smaller effect.
5. We suggest that whereas production of DOM_{tps} may be more important in controlling DOM dynamics in this ecosystem early in succession, mineral soil adsorption capacity appears to regulate DOM retention later in ecosystem development.
6. Furthermore, fine roots may play an increasingly fundamental role in the accumulation of SOM during ecosystem development, because fine roots become more deeply distributed (Uselman and others 2007a) and contribute an increasing proportion of total fine detrital DOM_{tps} production during ecosystem development.
7. We suggest that the water solubility of a substantial component of ecosystem NPP profoundly influences its potential for translocation and storage in mineral soil, leaching from the ecosystem, as well as availability for microbial respiration.

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